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## Observations on the behaviour of the primitively social bee, *Evylaeus* (= *Halictus*) *calceatus* Scop.

### I. Preliminary Report on the general life history

by

D. A. VLEUGEL

#### Introduction

Among the numerous groups of bees, the Sweat Bees (*Halictinae*) occupy a unique position. Some species are really solitary. Other species have more than one generation during the summer, but almost invariably only the females of the last generation survive the winter. The first summer generation (= second generation of the year) may have females and males or only females. In the latter case there is only a new brood, no generation. In this way there are several possibilities and this makes the life history of every more or less social species very interesting. An authoritative discussion of these problems has been written by PLATEAUX-QUENU (1967). MICHENER (1969) discussed the gradations of the social behaviour of *Halictine* bees in several publications on social behaviour in bees (the last in 1969).

In the present paper the general life history of *Evylaeus calceatus* is briefly reported as a preliminary note on the biology of this species. I studied *Evylaeus calceatus* in a small colony that was discovered in my garden at The Hague in April, 1943. I made observations during the spring, summer and autumn of that year and also during a period in 1944. After that I studied the literature which was nearly all in German (FABRE 1903, LEGEWIE 1925, STÖCKHERT 1923, NOLL 1931). Of late years a new start in the study of the *Halictinae* has been made by

BONELLI (1948), RAYMENT (1955), PLATEAUX-QUENU (1957—1967), SAKAGAMI & HAYASHIDA (1958 until now) and MICHENER (1958—1969). I am also glad to have had correspondance with Madame Dr. PLATEAUX-QUENU, Prof. SAKAGAMI and Prof. MICHENER. With the latter I also had a discussion at the International Entomological Congress in Vienna in 1960. I marked the bees individually, but it was not possible to dig up the nests, as the colony consisted of less than twenty nests so that I could not destroy any of them.

### The first generation

Only certain nests contained more than one ♀ (cf. VLEUGEL 1962). I discovered the nests on April 18th, 1943. Five nests contained 2 ♀ ♀ and one three. Some of the bees moved to other nests. As a rule this was done because the ant, *Lasius niger*, robbed their nests. I gave instances of these shifts in an earlier paper (1962). The nest openings were generally closed before sunset. However, there was considerable variation in the time of closing.

When there were two or more females in the nest, one of them guarded and defended the nest entrance. Occasionally females occupied the entrances of nests containing only one bee. I saw the *Evylaeus* collect on *Taraxacum officinalis* repeatedly. They also collected on other flowers. To say on which is not so simple. I suppose that they collect both pollen and nectar as PLATEAUX-QUENU (1960) found for *Halictus marginatus* Brullé. However, they often flew out of the nests without collecting at all and reentered without pollen. Detailed observations will be given afterwards.

One by one the nests were closed within a few days after April 18 and most were not opened again until the end of June. Of these closed nests I do not know, whether one or more "mothers" survived until the second generation (and/or the new brood of workers) appeared. In a few nests there was some activity until the appearance of the second generation, etc. These nests were opened and closed more or less regularly. I suppose that one or two "mothers" of the first generation survived so that they saw their "daughters" emerge and leave the nests. One or two of the mothers even appeared outside the nests now and then. In one of the nests I saw a guard on the last day of the season of the first generation (June 23rd).

### The second generation

On June 29th an unknown *Evylaeus* bee appeared which had emerged quite recently. The next day a nest that had been closed for more than five weeks was reopened. More ♀ ♀ emerged in the course of July. H. LODDER caught for me several fresh ♀ ♀ which also flew in the first half of July in South Limburg. According to FABRE (1903) the second generation consists only of ♀ ♀. He dug up hundreds of more or less developed females in July, but only one slender male. FAHRINGER (1910) also got only ♀ ♀ in July from the broods of *Evylaeus calceatus* which he cultivated from nests in the open. PLATEAUX-QUENU (1960, p. 100) called the summer males "quasi-absents". However, in 1961 she (PLATEAUX-QUENU 1963) found in a colony in the laboratory eight ♀ ♀ and one ♂. They emerged between June 7th and 26th, the ♂ being the last. Also NOLL (1931)



and WALCKENAAR (1817) found ♂♂ in July and KRIEGER (1894) found them from July to September. ALFKEN (1912, 1913) saw ♂♂ from July to October and WAGNER (1914) confirmed ALFKEN's data. HEDICKE (1922) found the ♂♂ from July until September. NOLL (l.c.) says further on: "Da aber nicht nur in den Monaten April und Mai, die zur Brutversorgung sicher ausreichen, sondern auch im Juni und Juli fliegende ♀♀ beobachtet sind, möchte ich annehmen, dass man noch eine rein weibliche Brut einschieben darf, wie sie FABRE festgestellt hat. Allerdings muss hier die Entscheidung durch Beobachtungen verbunden mit Ausgrabungen gebracht werden." I can say now that I found only one ♂ in July and I was almost sure that it was from my own colony. This was on the 11th of July, 1943 on *Taraxacum* blooming amidst the nests. On the other hand I did not find any ♂♂ anywhere in the country in July so far. I collected several years in different places, but chiefly in June and July at The Hague. Here I found another rather small colony of the species. So it appears that the second generation only contains few or very few ♂♂. For this reason it is theoretically possible to find in a colony the following inmates:

1. Nests with one or more mothers and one or more unfertilized daughters.
2. Nests with one or more mothers and one or more fertilized daughters.
3. Nests with one or more mothers and one or more fertilized and unfertilized daughters.
4. Nests with one or more unfertilized daughters, if as FABRE says, virgins produce a new brood.
5. Nests with one or more fertilized daughters.
6. Nests with one or more fertilized and one or more unfertilized daughters.

As a matter of fact the situation in *Evyleaus calceatus* seems to be similar to that in *Halictus duplex* Dalla Torre (SAKAGAMI & HAYASHIDA 1961). In this latter species males also appear in the spring broods, but in small numbers.

Because I have not dissected any, I cannot conclude which types of nests really occurred in the little colony in my garden. As a matter of fact I collected the ♂ I saw on July 11th and did not see any other at all. So it is probable that the ♀♀ which appeared after that date were not fertilized.<sup>1)</sup>

### The third generation

Throughout July and August there was activity in a small number of nests only. I observed the colony daily until July 23rd. During the summer holidays I was absent. I returned to The Hague from August 16th to 18th. There was activity only in one nest on these days. The other nests remained closed. After my subsequent return on August 31st, I saw a ♀ enter her nest. On Sept. 4th there was another ♀. Both were newly emerged females. On September 9th I had marked at least 10 females from two nests which were open regularly. After that more bees

<sup>1)</sup> Annotation of Professor MICHENER: "If the females of the second generation are mostly or all unfertilized, as seems probable, survival of the overwintered mothers (first generation) is very probable, and their eggs probably produce not only the so-called second generation, but also at least the females of the third. In this case the terms "second generation" and "third generation" are misnomers and are really first and second broods of one annual generation."

emerged during the next weeks. On Sept. 7th there were a ♀ and a ♂ in the jar I had placed over a nest entrance; they were newly emerged. The ♂ did not try to copulate in the jar. I did not see other ♂ ♂ leave the nests. In my opinion the other ♂ ♂ had emerged in the last third of August during my absence. It must be concluded that ♂ ♂ do not return to the nests as the ♀ ♀ regularly did.

I have collected a number of individuals of both sexes in several places in the Netherlands. Nearly all the males were caught after August 20th. I observed also in a large colony at Kattendijke, province of Zeeland. This was between August 20th and August 30th. I saw a number of ♂ ♂ flying to and fro in the colony. I saw no copulations, as far as I remember, but I was there for a short time only. However, I saw a copulation in a clover field where many ♂ ♂ and ♀ ♀ were present. I have only three specimens of *Evylaeus calceatus* males caught before August 20th. They were: 11.VIII.1946, Arnhem; 12.VIII.1943, Wemeldinge; and 19.VIII.1946 Kwadendamme. All were fresh males, apparently of the third generation. So it appears that few males emerge before August 20th. Because the ♂ ♂ usually emerge before the ♀ ♀, I have probably missed the ♂ ♂ of the nests in my garden at The Hague.

I cannot say with certainty where the ♀ ♀ overwintered. From the observations noted below, I believe that part of them remained in the nests, but that others stayed in other places during the winter.

#### First generation, next spring

On April 11th and 12th, 1944, an *Evylaeus calceatus* had made an opening in the place of a nest of the preceding year. On April 13th I saw the first *calceatus* in my garden on *Taraxacum*. I do not know whether it was one of the bees of my own colony. I marked it white. She dug herself into the colony. She had probably forgotten the exact place of her nest, for a nest entrance was left open in a similar place near a stone one decimeter from the location where the bee had disappeared into the ground. On April 14th the former nest stood open for the first time this year. Probably another female had overwintered there. Although a bee remained some time in the new nest, regular nesting activity did not follow.

On April 18th I saw a *calceatus* female, marked orange the preceding autumn, flying around. It was a bee from my colony. However, no nest entrance was open, so that it is probable that this bee stayed elsewhere during the winter. This bee was never seen again. On April 30th a *calceatus* female disappeared into a nest entrance on the site of a nest of the year before. It was unmarked. This bee brought pollen to this nest for the first time on May 13th. There was some activity in this nest until May 29th, when it was very hot; on that day I found the bee dead in the jar I had placed over the nest to study the behaviour of the bee. The temperature in this jar in the sun was at least 50° C. After this I did not see any *Evylaeus calceatus* female at all which seemed to belong to this colony. Only now and then I saw one or two stragglers on the flowers.

Apparently a new colony was begun in the garden in the spring of 1943. After slightly more than a year, however, it had already died out. Never did any young bees emerge in the new colony in 1944; I looked for them intensively during the



whole summer and even in the next spring. Now and then two, even three, females of *Evylaeus calceatus* were seen "playing" together in spring, but so far no other new colony has been started in my garden.

### Discussion

SAKAGAMI & MICHENER (1962) say on p. 20 of their valuable book on the nest architecture of the Sweat Bees (Halictinae): "halictines often concentrate their nests within relatively limited areas, forming so-called colonies or pseudocolonies for which the word aggregation seems more appropriate." It seems to me that it is premature to decide at this time which word is most appropriate. In the concentrations of nests of *Evylaeus calceatus* in my garden (VLEUGEL 1962), there was some intermingling between bees of different nests. It is possible that this intermingling of bees between different nests of a colony (aggregation) is even greater in some species. This was for instance the case in *Lasioglossum* (*Dialictus*) *versatum* (MICHENER 1966 and 1966a) and *Lasioglossum zephyrum* (BATRA 1966). KNERER & PLATEAUX-QUENU (1966) found it also in *Halictus ligatus* Say in Canada. I think that we should not decide to speak of a colony or an aggregation, before this problem has been studied thoroughly in a number of species of Halictinae. Where this intermingling does not occur, as for instance in *Andrena vaga* (VLEUGEL 1947), it is right to speak of an aggregation. However, there are very few species of bees which have been studied so precisely, with the help of marked bees, that we know which form aggregations and which real colonies.

There is another difficult question in the Halictinae. Are the succeeding "generations" of *Halictus* etc. real generations or only broods? I think this cannot be decided either so far. I found only one male in the summer "generation" of the colony of *Evylaeus calceatus* I studied. And there appear to be few, if any males in summer. But a few males may fertilize many ♀ ♀ of course. This is actually found in *Halictus duplex* (SAKAGAMI & HAYASHIDA 1961). On the other hand PLATEAUX-QUENU (1963) found, as I did( that there was only one ♂ in the nest she studied. However, the 8 ♀ ♀ she dissected from this nest, were not fertilized. Perhaps the ♂ ♂ do not copulate with ♀ ♀ from their own nest. It is also possible that the bees show a behaviour in the laboratory which is not quite normal. I think this question should be studied further, before one can decide whether the bees which appear after a period of rest in the nests are broods or generations. On the other hand it seems that in some colonies (aggregations) there are broods and generations side by side (*Halictus duplex*). In other cases there may be real broods, e.g. with *Halictus marginatus* (PLATEAUX-QUENU 1959). Another possibility is that there are real generations as FABRE (1903) and RAYMENT (1955) believed.

### Summary

A little colony of less than twenty nests of *Evylaeus* (= *Halictus*) *calceatus* Scopoli was studied by the writer in 1943 and the spring of 1944. In the spring generation of 1943 some nests contained one adult ♀, others two or three. In a very few nests there was some slight activity before the appearance of the second generation (brood) at the end of June and during July. There was only one ♂

in the second generation (brood); the other bees emerging in June and July were all ♀ ♀. Most nests were not opened again in June and July, so that probably in these nests no broods were raised. In some nests a third generation (brood) appeared at the end of August and in the course of September. It consisted of ♂ ♂ and ♀ ♀. This generation was not found under laboratory conditions by PLATEAUX-QUENU (1963).

In the next spring very few *Evylaeus calceatus* ♀ ♀ were seen. Only one marked individual of the preceding autumn was recovered. From the behaviour of the ♀ ♀ it was concluded that some overwintered in the colony, others elsewhere. The activity was very slight. It ceased altogether when on a hot day in May the only surviving active female died.

MICHENER (1969) discussed the gradations of social behaviour of Halictine bees in several publications on social behaviour in bees (the last in 1969). An authoritative discussion of these problems has been written by PLATEAUX-QUENU (1967).

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